

INFRASPECIFIC CLASSIFICATION OF *CHLORACANTHA SPINOSA*
(BENTH.) NESOM (ASTERACEAE) ASTEREAEE

Scott D. Sundberg

Department of Botany, KB-15, University of Washington, Seattle,
Washington 98195 U.S.A.

ABSTRACT

Four allopatric varieties of *Chloracantha spinosa* (Benth.) Nesom are recognized, based on head size, number of phyllaries and florets, phyllary shape, anther length, abundance of stem spines, spine length, achene length, pappus bristle length, and characteristics of the terminal cells of the pappus bristles.

KEY WORDS: Asteraceae, Astereae, *Chloracantha*, *Aster spinosus*, North America, Central America

Arguments for the placement of *Aster spinosus* Benth. in the monotypic genus *Chloracantha* Nesom, Suh, Morgan, Sundberg, & Simpson are presented in Nesom, *et al.* (1991) in this volume. The transfer of the species is based on its distinctive vegetative morphology and on studies of chloroplast DNA restriction fragment length polymorphisms that demonstrate a closer affinity to *Boltonia* and possibly to *Heterotheca* rather than to *Aster* or *Erigeron*, to which it has been allied in the past (Sundberg 1986). In this paper the infraspecific classification of *Chloracantha spinosa* (Benth.) Nesom is presented.

Chloracantha spinosa is a widespread weed in the southern United States from southern California to southern Louisiana, ranging to the north in Arizona, New Mexico, and Texas with scattered localities in Nevada, Utah, and Oklahoma, and to the south throughout México to northwestern Panamá (Fig. 1). Historically, three varieties have been recognized within the species. Brandegee (1917) segregated *Aster spinosus* var. *spinossimus* Brandegee of Baja California Sur from the typical variety on the basis of its numerous rigid spines and larger heads. McVaugh (1972) treated variety *jaliscensis* McVaugh as a distinct taxon, citing lack of spines, leafiness at anthesis, differences in phyllary number, phyllary morphology, and differences in pappus and achene length. In this paper, variety *strictospinosa* Sundberg is described. Its stout, ascending

spines are not found elsewhere within the species and it has a combination of other morphological features that is unique within the species.

Two pairs of closely related varieties of *Chloracantha spinosa* are readily apparent. Varieties *jalscensis* and *strictospinosa*, which form one pair, have shorter and more delicate pappus bristles, broader phyllaries with wider hyaline margins and rounded apices, shorter disk florets, fewer ray florets, and are found in more moist, tropical regions than varieties *spinosa* and *spinosissima*.

TAXONOMIC TREATMENT

Chloracantha spinosa (Benth.) Nesom, *Phytologia* 70:378. 1991. Based on *Aster spinosus* Benth., *Pl. Hartw.* 20. 1839. TYPE: MÉXICO. *Hartweg 148* (HOLOTYPE: K, photograph of holotype MICH!, TEX!; Isotypes: BM!, CGE, GH!). McVaugh (1984) lists the type from Aguascalientes. *Leucosyris spinosa* (Benth.) E. Greene, *Pittonia* 3:244. 1897.

Perennial, shrublike herbs, from stout rhizomes. Stems erect, 0.5-2.5 m tall, much branched, striate, often angled on smaller branches, glabrous, 5-25 mm in diameter and woody at the base, usually with stout ascending or curved-divaricate spines below and unarmed branches above, sometimes spiny or unarmed throughout. Leaves basally disposed on main stem, usually absent at anthesis, oblanceolate to spatulate, 1-4 cm long, sessile, venation brochidromous, with one prominent midvein, glabrous except for sparsely ciliate margins and occasional trichomes on the upper surface, trichomes uniseriate, appressed, with attenuate or filiform terminal cell, 0.1-0.2 mm long; margins entire or with 1-5 small teeth, apically acute to rounded; leaves of lateral branches lanceolate, grading into bracts in the capitulescence. Capitula numerous in cymose capitulescence, with wiry, ascending, naked branches and scattered capitula terminating bracteate branchlets 2-8(-11) cm long or disposed towards the upper side of the branch on branchlets 0.1-3 cm long, erect in bud; involucre broadly cylindrical turbinate to subhemispherical, rounded and somewhat fleshy at base or with a shallow circular depression surrounding the peduncle (larger heads), 4.0-7.5 mm tall; phyllaries 20-55, imbricated, in 3-5 series, glabrous, herbaceous, with (1-)3(-5) golden brown nerves, subulate to linear-lanceolate (elliptic-lanceolate), margins hyaline, sometimes expanded above, subentire to conspicuously ciliate, apically acute to rounded. Ray florets 10-33 in 1 series; corollas white, sometimes tinged with purple at tips when young, drying white, ligulate portion 3.5-7.7(-10.2) mm long, (0.5-)0.7-2 mm wide tube moderately puberulent. Disk florets (13-)20-70; corollas yellow, sometimes tinged with green when fresh or drying purplish, (3.2-)3.5-6.0 mm long; limb tubular-funnelform but somewhat asymmetrical, slightly gibbous adaxially, expanded 0.6-1 mm above the insertion of the filaments, 1.8-3.5 mm long; lobes asymmetrical, the abaxial ones longer than the adaxial, acute, erect, 0.5-1 mm long; tube puberulent; style branches 0.9-1.1(-1.5) mm long,

appendage acute to deltoid, 0.1-0.2 mm long; style base bulbiform; anthers 1.1-2.0 mm long, distal 1/3 of filament collar cells usually with nodular thickenings; anther appendage lanceolate-ovate. Achenes glabrous, fusiform, somewhat radially compressed, (1.2-)1.5-3.5 mm long; tan with 5-6, conspicuous, golden brown ribs; carpodia 4-8 cells high, grading into the body of the achene; pappus of 30-60 white to buff subequal bristles 2.5-6.0(-6.5) mm long, often with a few outer bristles 1-2 mm long.

DISTRIBUTION: Widespread, weedy subshrub in moist areas along irrigation ditches, streams, and freshwater swamps, sometimes phreatophytic in drier habitats; southern California to southern Louisiana; north to Arizona, New Mexico, and Texas, with scattered localities in Nevada, Utah, and Oklahoma; south through México to northwestern Panamá (Fig. 1; a list of specimens examined is available from the author and is deposited at TEX).

KEY TO VARIETIES

Pappus bristles 4.5-6.0(-6.5) mm long, delicate, with cells near tips tightly appressed; disk florets (21-)30-70; ray florets 20-33; middle phyllaries subulate to lanceolate, apex acute to attenuate, occasionally rounded by an extension of the narrow hyaline margins.

Plants usually sparsely spiny, with many spineless wandlike branches above, spines usually shorter; achenes (1.2-)1.5-2.0(-2.3) mm long; involucre 4.0-5.5(-6.0) mm tall, with 25-45(-52) phyllaries; disk florets (21-)25-50(-55); ligules 3.5-5.0(-7.0) mm long; anthers 1.1-1.5 mm long; widespread in southern states of the U.S., lowlands of Sonora and Sinaloa, Baja California Norte, and the central plateau of México.1. var. *spinosa*.

Plants densely spiny; achenes 2.8-3.5 mm long; involucre (5.0-)6.5-7.5 mm tall, with (35-)45-55 phyllaries; disk florets (40-)50-70; ligules 5.2-7.7(-10.2) mm long; anthers 1.5-2.0 mm long; Baja California Sur.2. var. *spinosissima*.

Pappus bristles 2.5-3.5(-3.9) mm long, coarser, with cells near tips divergent at ends and relatively more dense; disk florets (13-)18-30(-34); ray florets 10-23; middle phyllaries lanceolate elliptic to elliptic, apex rounded.

Plants usually without spines; Sierra Madre Occidental in Sonora and Sinaloa to western Durango, Nayarit, and Jalisco.3. var. *jaliscoensis*.

Plants densely spiny; Michoacán, México, to Panamá.4. var. *strictospinosa*.

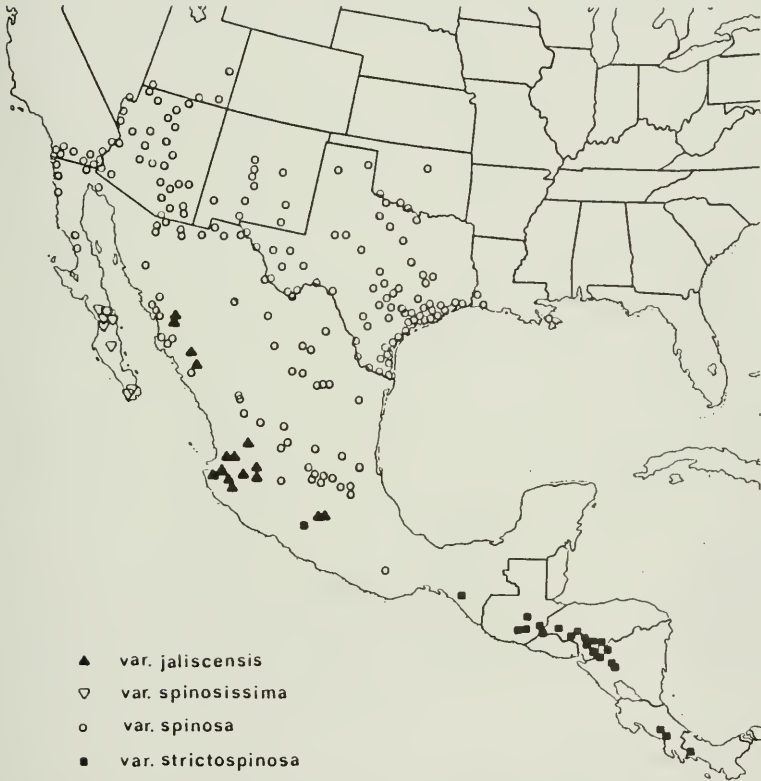


Figure 1. Distribution of *Chloracantha spinosa*.

1. *Chloracantha spinosa* (Benth.) Nesom var. *spinosa*

Plants usually moderately spiny at base, occasionally copiously spiny or unarmed. Involucres 4.0-5.5(-6.0) mm tall; phyllaries 25-45(-52), imbricated in 4-5 series, middle phyllaries subulate to lanceolate, apex acute or occasionally somewhat rounded by a hyaline margin. Ray florets 20-33, ligulate portion 3.5-5.0(-7.0) mm long, (0.5-)0.7-1.3 mm wide. Disk florets (21-)25-50(-55); corollas 4.0-5.2(-6.0) mm long, lobes 0.5-0.7(-1.0) mm long, limb (1.8-)2.4-3.0 mm long; anthers 1.1-1.5 mm long. Achenes (1.2-)1.5-2.0(-2.3) mm long; pappus bristles 4.5-6.0(-6.5) mm long. Chromosome number $n = 9$ (Table 1).

DISTRIBUTION: Widespread on moist loam or sandy soil along streams, irrigation ditches, and freshwater swamps; southern California to Louisiana, north to Nevada, Utah, and Oklahoma, south in México to the state of México; collections from cultivated areas in the Valley of Oaxaca may be introductions from farther north.

This variety is highly variable in spininess and the abundance of leaves at flowering time. There is apparently no correlation between these characters and geographical distribution. Populations from the Imperial Valley and the lower Colorado River of southern California and Arizona are unusual in having fleshy stems, larger heads, and short branchlets in the capitulescence. In this area, the plants are often phreatophytic, growing in areas that are frequently flushed of salt buildup (Burk 1977). Their growth form may be partly due to high salinity in these areas. A collection (Keil, et al. 16615) from the coast of Sonora north of Guaymas (in "Maytenus-dominated shrubland and tidal mudflat area") is intermediate between var. *spinosa* and var. *spinosissima*. It has the short achenes of the former, has large heads of the latter, and is intermediate between the two in ligule length, anther length, and spininess. It was collected near sea level, close to the southern limit of a portion of the Sonoran Desert that Shreve & Wiggins (1964) termed the "Central Gulf Coast." This region also encompasses part of the eastern coast of Baja California, including a portion of the range of var. *spinosissima*. It may be a salt form of variety *spinosa* or may be a product of gene exchange between the two varieties.

2. *Chloracantha spinosa* (Benth.) Nesom var. *spinosissima* (Brandege)

Sundberg, *comb. nov.* BASIONYM: *Aster spinosus* Benth. var. *spinosissimus* Brandege, Univ. Calif. Publ. Bot. 6:375. 1917. TYPE: MÉXICO. Baja California Sur: San Gregorio, 1 Feb 1889, Brandege s.n. (HOLOTYPE: UC!; Photograph of holotype: TEX!; Isotypes: PH!, US!).

Involucres (5.0-)6.0-7.5 mm tall; phyllaries (35-)45-55, imbricated in 4-5(-6) series; middle phyllaries subulate to lanceolate, with a narrow, hyaline, often purple tinged margin, apex acute to attenuate. Ray florets 20-28; ligulate portion 5.2-7.7(-10.2) mm long, 1.3-2.0 mm wide. Disk florets (40-)50-70; corollas (4.5-)5.0-6.0 mm long, lobes 0.7-1.0 mm long, limb 2.7-3.5 mm long;

TABLE 1. Chromosome numbers of *Chloracantha spinosa*. All counts are $n = 9$. Counts followed by literature citations were reported as *Aster spinosus*; others are unpublished counts by SS. * = mitotic count (others meiotic counts); ! = voucher seen; SS = S. Sundberg.

Chloracantha spinosa var. *spinosa*:

USA: Arizona: Coconino Co.: just below Lee's Ferry, *Raven 13132!* (Raven, *et al.* 1960); Marble Canyon, *Brown & Parfitt 900!* (Brown & Clark 1979); Maricopa Co.: 1.2 mi W of Buckeye, *SS & Hardison 2110!*; 3 mi E of Buckeye, *SS & Hardison 2111!*; E of Buckeye, Hwy. 85 & Watson Rd, *SS & Lee 2687!*. California: Imperial Co.: canal on W outskirts of El Centro, *Raven 16833!* (approx. count: Solbrig, *et al.* 1964); *coll. unknown (Huziwara 1965); N of Brawley, Hwy. 86, *SS 2085!*; just N of Imperial City along Hwy. 86, *SS 2086!*; 5.2 mi W of Westmorland along Hwy. 86, *SS & Hardison 2103!*; E end of Brawley, *SS & Hardison 2104!*; 7.9 mi S of jct. of Hwy. 111 & Hwy. 78 *SS & Hardison 2105!*; E of Calexico along Hwy. 98, *SS & Hardison 2106!*; S of Niland, *SS 2672!*; E of Brawley along Hwy. 78, *SS 2678!*. Texas: Bee Co.: S of Beeville, Hwy. 181, *SS & Hardison 2163!*; Reeves Co.: Balmorhea, *Sikes 90!* (Powell & Sikes 1970); Travis Co.: Austin, *Watson 550!* (Watson 1973); Austin, *SS 1206!*, *SS 1356!*.

MÉXICO: Chihuahua: W of Presidio, *SS & Lavin 2710!*. Coahuila: 5.5 mi E of Nazareno, *Keil & McGill 8010!* (Keil & Stuessy 1975). Durango: Durango, *King 3727!* (Turner, *et al.* 1961); 13 mi N of Durango, *King 3753!* (Turner, *et al.* 1961). Oaxaca: 10 mi NE of Oaxaca, *King 3518!* (Turner, *et al.* 1961).

Chloracantha spinosa var. *jalicensis*:

MÉXICO: Jalisco: W of Ameca, *SS & Lavin 2952!*; 18 km N of Talpa, *Lott, et al. 1346!*; just N of El Jacal, *Ayers, et al. 266!*.

anthers 1.5-2.0 mm long. Achenes 2.8-3.5 mm long; pappus bristles 40-50, white, delicate, 4.8-5.5 mm long, outer cells of bristles appressed.

DISTRIBUTION: Baja California Sur, from hills W of Bahía Concepción to the south, on alluvial soil in arroyos, elev. 250-700 m.

Variety *spinosissima* is a densely spiny, large headed counterpart of the widespread, weedy variety *spinosa*.

3. *Chloracantha spinosa* (Benth.) Nesom var. *jaliscensis* (McVaugh) Sundberg, *comb. nov.* BASIONYM: *Aster spinosus* Benth. var. *jaliscensis* McVaugh, Contr. Univ. Michigan Herb. 9:363. 1972. TYPE: MÉXICO. Nayarit: among rocks in the stream above La Laguna, 3 km NE of Santa María del Oro, elev. ca. 1000 m, 16 Sep 1960, *McVaugh 19049* (HOLOTYPE: MICH!; Photograph of holotype: TEX!; Isotypes: DUKE!, ENCB!, LL!, US!).

Erigeron ortegae S.F. Blake, Proc. Biol. Soc. Wash. 37:55(-56). 1924.

TYPE: MÉXICO. Sinaloa: Balboa, Jan 1923, *Ortega 4974* (HOLOTYPE: US!).

Plants usually unarmed throughout, occasionally with divergent spines near base. Involucres 4.5-5.1(-5.5) mm tall; phyllaries 20-32(-37), imbricate in 4-5 series, middle phyllaries elliptic-lanceolate, apex rounded. Ray florets 10-20, ligulate portion 4.5-6.7 mm long, 1.2-1.7 mm wide. Disk florets (13-) 18-25(-34); corollas 3.1-4.0(-4.5) mm long, lobes 0.5-0.9 mm long, limb 2.0-2.5(-3.2) mm long; anthers 1.1-1.4 mm long. Achenes 2.1-2.8(-3.4) mm long; pappus bristles 2.5-3.5 mm long. Chromosome number $n = 9$ (Table 1).

DISTRIBUTION: Western slope of the Sierra Madre Occidental in southern Sonora to Sinaloa and western Durango, Nayarit, and Jalisco.

About half of the herbarium specimens of this variety are leafy, flowering shoots. These specimens usually show signs of damage due to grazing. Plants of var. *spinosa*, when repeatedly pruned, often have a few leaves at flowering time, suggesting that the leafiness of many collections of var. *jaliscensis* may be due to grazing. At the margins of distribution of var. *jaliscensis* occur forms that are intermediate between this variety and others. The only spiny collections of the variety are from such areas. Thus, collections from Cofradía (vicinity of Culiacán, Sinaloa, 20 Oct 1904, *Brandege s.n.* at UC), from Tamazula, Durango (*Gentry 5260* at ARIZ, DS, GH, MEXU, MICH, MO, NY, UC) and from La Junta, Estado de México (*Matuda 29808* at NY, US) have the typical short pappus, long achenes, and rounded phyllaries but are spiny. One collection (*Gentry 505* at DS) from the vicinity of Alamos, Sonora, includes stems that appear to be typical of var. *jaliscensis* and a single stem that is intermediate between var. *jaliscensis* and var. *spinosa*. This specimen agrees in all ways with my circumscription of var. *jaliscensis* except in having pappus bristles that are up to 4.5 mm long.

4. *Chloracantha spinosa* (Benth.) Nesom var. *strictospinosa* Sundberg, var. nov. TYPE: HONDURAS. Dept. Morazán: Río Caparosa, near Zamorano, flowers white, shrub to 1 m, on rocks, alt. 800 m, 1 Jan 1963, *Williams 23285* (HOLOTYPE: LL!; Isotypes: ARIZ!, DS!, F!, MEXU!, MICH!, MO!, NY!, PH!, UC!, US!).

Achaenia 2.2-3.0 mm longa, setae pappi 2.9-3.5(-3.9) mm longae; a *Chloracanthae spinosae* (Benth.) Nesom var. *jaliscensi* (McVaugh) Sundberg plantis crebre spinosis spinis validis differt.

Plants densely spiny with stout, ascending spines; stems divaricately branched. Involucres (4.5-)5.0-6.0(-6.5) mm tall; phyllaries 20-30(-35), imbricated in 3-4 series; middle phyllaries lanceolate-elliptic, apex rounded. Ray florets 14-23, ligulate portion (4.4-)5.2-6.0 mm long, 1.2-2.0 mm wide. Disk florets 22-30 (-34); corollas (3.2-)3.5-4.3 mm long, lobes 0.5-0.7 mm long, limb (1.8-)2.4-3.0 mm long; anthers 1.2-1.5 mm long. Achenes 2.2-3.0 mm long; pappus bristles 2.9-3.5(-3.9) mm long.

DISTRIBUTION: Michoacán, México, through Guatemala, El Salvador, Nicaragua, and Costa Rica to northwestern Panamá. Illustration: D'Arcy (1975): fig. 35.

Additional specimens examined: COSTA RICA: Río Virilla, *Allen 578* (F); Río Virella, *Pittier 10* (GH, US); Río Torres, Cartago, *Smith 4870* (F, GH, NY, US); Rancho Flores, *Tonduz 2179* (US); Río Tirriti, San Jose, *Tonduz 7060* (F, GH, MO, NY, US); Río Tiliri at Anones bridge, *Tonduz 7327* (DS, F, GH, MICH, NY, UC, US).

EL SALVADOR. Río Guaza, *Calderon 1933* (GH, US).

GUATEMALA. Casillos, Río San Rafael, *Aguilar 343* (F); Dept. Quiche, *Aguilar 804* (F); Agua Caliente, *Greenman & Greenman 5924* (GH, MO); El Rancho, *Kellerman 5328, 7646* (F); Paso de Jelha, *Pittier 1821* (F); Santa Rosa, *Smith 3424* (F); Santa Rosa, *Smith 4210* (F, GH, NY, US); near Jutiapa, *Standley 60543* (F); northwest of Jutiapa, *Standley 76288* (F); near Zacapa, *Standley 72089* (F); vicinity of Jutiapa, *Standley 75833* (F); near Jalapa, *Standley 77159* (F, NY, US); 4-6 miles north of Chiquimula, Río Chiquimula, *Steyermark 30279* (F); vicinity of Jalapa, *Steyermark 32131* (F).

HONDURAS. Escuela Panamericana de Agricultura, Zamorano, *Carlson 3190* (F); Río Choluteca *Carlson 2597* (F); Siguatepeque, Comayagua, *Clewell 3731* (MO, US); Yeguaré River, Morazán, *Glassman 2013* (F, NY, TEX, UC); 5 km E of Zamorano, Morazán, *Meyer 9942* (MO); Choluteca River, near Ojo de Agua, El Paraiso, *Morton 7144* (F, US); Río Yeguaré, *Molina 5031* (F); Río Guacerique, NW of Tegucigalpa, Morazán, *Molina 18572* (F, GH, NY, US); Río Mejojote, 9 km from Gracias, Lempira, *Nelson, et al. 202* (MO); Río Yeguaré, *Rodriguez 970* (F); Santa Inés, *Rodriguez 1525* (F); Las Casitas, *Standley, et al. 584* (F); Río Humuya, *Standley, et al. 5432* (F); Siguatepeque,

Standley, et al. 6433 (F); San Marcos de Colón, *Standley 15807* (F); Marcala River, La Paz, *Standley 24275* (F, NY, US); 2 miles west of Guinope, *Williams & Molina 10321* (F); Río Yeguaré near Casitas, El Paraiso, *Williams & Molina 11058* (F, GH).

MEXICO. Chiapas: Rancho La Aurora, *Sanchez 1078* (ENCB, UC); Mihoacán: cliff over Balsas River, *Hinton 5610* (GH, MEXU, MO, NY, US).

NICARAGUA: 6.5 km from Ocotol, Nueva Segovia, *Moreno 14444* (TEX); La Estanzuela, Estelí, *Moreno 24379* (TEX); Santa Maria do los Pinos, Nueva Segovia, *Moreno, et al. 24764* (TEX); on rocks in Río Estanzuela, SW of Estelí, Estelí, *Williams & Molina 20187* (DS, UC); La Guava, Estelí River, Estelí, *Williams & Molina 42478* (US, MICH).

PANAMÁ: Valley of upper Río Chiriquí Viejo, Chiriquí, *White & White 108* (MO).

This variety is most closely related to variety *jahiscensis*, sharing a short pappus and lanceolate elliptic to elliptic middle phyllaries. It may be distinguished from the latter in its spininess (dense, usually ascending in var. *strictospinosa* vs. usually absent, or divergent when present in var. *jahiscensis*) and its geographical distribution. Variety *strictospinosa* usually has broader hyaline phyllary margins and longer, more numerous disk florets, although there is a great deal of overlap in these characters. The new variety is named "strictospinosa" for its rigid spines.

ACKNOWLEDGMENTS

This research was supported in part by National Science Foundation Grant BSR-8313002. I wish to thank Billie L. Turner, John Strother, Guy L. Nesom, Almut G. Jones, and Arthur Cronquist for advice on early versions of the manuscript, Thomas Lammers for herbarium investigations at P, and the curators of herbaria at ARIZ, ASU, BM, C, CAS, DS, DUKE, ENCB, FLAS, FSU, FTG, GH, JEPS, ILL, LL, LSU, MEXU, MICH, MO, NCU, NLU, NMC, NO, NY, PII, POM, RSA, TEX, UC, US, USF, W, WIS, WTU, and XAL for specimen loans or use of the collections. The manuscript was reviewed by Billie L. Turner and Guy L. Nesom.

LITERATURE CITED

- Brandege, T.S. 1917. *Plantae Mexicanae Purpusianae VIII*. Univ. California Publ. Bot. 6:363-375.
- Blake, S.F. 1924. Eight new Asteraceae from Mexico, Guatemala, and Hispaniola. Proc. Biol. Soc. Wash. 37:55-62.

- Brown, G.K. & D. Clark. 1979. In IOPB Chromosome Number Reports LXV. *Taxon* 28:627-637.
- Burk, J.H. 1977. Sonoran Desert vegetation. In *Terrestrial Vegetation of California* (eds. M.G. Barbour & J. Major). New York: John Wiley & Sons.
- D'Arcy, W.G. 1975. Flora of Panama, part IX. (Family 184. Compositae). *Ann. Missouri Bot. Gard.* 62:1004-1032.
- Huziwara, Y. 1965. Chromosome analysis in the tribe Astereae. *Jap. J. Genet.* 40:63-71.
- Keil, D.J. & T.F. Stuessy. 1975. Chromosome counts of Compositae from the United States, Mexico, and Guatemala. *Rhodora* 77:171-195.
- McVaugh, R. 1972. *Compositarum Mexicarum Pugillus*. *Contr. Univ. Michigan Herb.* 9:360-484.
- McVaugh, R. 1984. *Flora Novo-Galiciana*. Vol. 12. Compositae. University of Michigan Press, Ann Arbor.
- Nesom, G.L., Y. Suh, D.R. Morgan, S.D. Sundberg, & B.B. Simpson. 1991. *Chloracantha*, a new genus of North American Astereae (Asteraceae). *Phytologia* 70:371-381.
- Powell, A.M. & S. Sikes. 1970. Chromosome numbers of some Chihuahuan Desert Compositae. *Southw. Naturalist* 15:175-186.
- Raven, P.H., O.T. Solbrig, D.W. Kyhos, & R. Snow. 1960. Chromosome numbers in Compositae. I. Astereae. *Amer. J. Bot.* 47:124-132.
- Shreve, F. & I.L. Wiggins. 1964. *Vegetation and flora of the Sonoran Desert*. Stanford: Stanford University Press.
- Solbrig, O.T., L.C. Anderson, D.W. Kyhos, P.H. Raven, & L. Rudenberg. 1964. Chromosome numbers in Compositae V. Astereae II. *Amer. J. Bot.* 51:513-519.
- Sundberg, S.D. 1986. The systematics of *Aster* subg. *Oxytripolum* (Compositae) and historically allied species. Ph.D. dissertation, University of Texas at Austin.
- Turner, B.L., W.L. Ellison, & R.M. King. 1961. Chromosome numbers in the Compositae IV. North American species, with phyletic interpretations. *Amer. J. Bot.* 48:216-223.
- Watson, T.J., Jr. 1973. Chromosome numbers in Compositae from the southwestern United States. *Southw. Naturalist* 18:117-124.